A New Species of Iochroma (Solanaceae) from Ecuador

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ABSTRACT. *Iochroma baumii* S. D. Sm. & S. Leiva (Solanaceae) is described from the cloud forests of Napo in northern Ecuador. We provide a summary of the phylogenetic relationships and recent taxonomic changes in *Iochroma* Benth. and related genera and discuss the phylogenetic placement of this newest species. *Iochroma baumii* shares its geographic distribution and many floral features with its closest relatives *I. calycinum* Benth., *I. fuchsioides* (Bonpl.) Miers, and *I. gesnerioides* (Kunth) Miers, but its deep blue flowers with involute corolla lobes, which appear in clusters along older branches, make it easily distinguishable from its congeners.

Resumen. Se describe *Iochroma baumii* S. D. Sm. & S. Leiva (Solanaceae) de los bosques nublados del norte de Ecuador. Presentamos un resumen de las relaciones filogenéticas y cambios taxonómicos más recientes en *Iochroma* Benth. y los géneros afines. También discutimos la relaciones filogenéticas entre esta nueva especie y las otras especies de *Iochroma*. *Iochroma baumii* comparte su distribución geográfica y características florales con las especies hermanas: *I. calycinum* Benth., *I. fuchsioides* (Bonpl.) Miers y *I. gesnerioides* (Kunth) Miers, pero, por sus flores azúloscuro con lóbulos involutos, que aparecen agrupadas en ramas maduras, se distingue fácilmente de las otras especies de *Iochroma*.

Key words: Andean, Ecuador, Iochroma, Iochrominae, IUCN Red List, Solanaceae.

Iochroma Benth. (Solanaceae) is a genus of around 25 species of unarmed shrubs and treelets distributed from Colombia to Peru (Shaw, 1998; Hunziker, 2001; Smith & Baum, 2006, Leiva, 2009). A member of Physaleae Miers (Olmstead et al., 2008), the genus is perhaps best known for its colorful, tubular flowers, and some species are cultivated as ornamentals (Shaw, 1998). Iochroma species are most common in

cloud forest gaps and disturbed areas between 1800 and 2800 m, and their flowers are pollinated by hummingbirds and a range of insects (Smith et al., 2008).

Recent phylogenetic work has clarified relationships between *lochroma* and the allied genera Acnistus Schott, Dunalia Kunth, Eriolarynx (Hunz.) Hunz., Saracha Ruiz & Pav., and Vassobia Rusby, which together comprise Iochrominae sensu Olmstead et al. (1999, 2008). Most of the species of *Iochroma* fall into a core clade with four subclades, designated with the letters A, C, L, and F (Smith & Baum, 2006; Table 1). There is an additional small clade of five *Iochroma* species (the U clade) that appears closely related to core clade in some gene trees and more distant in others (Smith & Baum, 2006). Finally, three species traditionally placed in Iochroma are actually more closely related to species in other genera, e.g., Dunalia, Eriolarynx, and Datura L. (Smith & Baum, 2006; Olmstead et al., 2008; Table 1).

Despite these advances in understanding phylogenetic relationships, much remains to be discovered about the ecology, biogeography, and evolutionary history of *Iochroma*. The most recent treatment of Iochroma included only 15 species (Shaw, 1998), but 12 new species have been described since 1995 (Leiva, 1995, 2005, 2006, 2007, 2009; Leiva et al., 1998; Leiva & Quipuscoa, 1998; Lezama et al., 2007). Many of these are known exclusively from a single collection or a single locality, and several have not been included in phylogenetic analysis (Table 1). Some of these new taxa are known to be products of interspecific hybridization (Smith & Baum, 2006; Smith et al., 2008; Table 1) as interspecific crossability is widespread in the Iochrominae (Smith & Baum, 2007). Still, the extent of contact and hybridization among *Iochroma* species in nature is largely unknown. In addition to the taxa listed in

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492 Novon

Table 1. Species of *Iochroma* and their phylogenetic placement. In addition to the species included in the most recent treatment (Shaw, 1998), we list the 12 species recently described from Peru by S. Leiva. Clade letters refer to the phylogenetic placement in Smith and Baum (2006), with an asterisk after the clade denoting placement predicted from morphology. Known or suspected hybrids were not placed in clades nor were taxa excluded, based on the phylogeny (Smith & Baum, 2006). The C, L, F, and U clades contain only species traditionally placed in *Iochroma*, whereas the A clade also contains the monotypic genus *Acnistus* Schott. Country abbreviations are as follows: Argentina (ARG), Bolivia (BOL), Colombia (COL), Ecuador (ECU), Peru (PER); SDS and SLG refer to the author initials.

Clade	Species	Distribution	Notes
A	I. confertiflorum (Miers) Hunz.	ECU, PER	
\mathbf{A}	I. edule S. Leiva	PER	
A	I. ellipticum (Hook. f.) Hunz.	ECU	
A	I. peruvianum (Dunal) J. F. Macbr.	PER	
A	I. salpoanum S. Leiva & Lezama	PER	
A^*	I. smithianum K. Lezama, Limo & S. Leiva	PER	known only from type collection
A*	I. tupayachianum S. Leiva	PER	
C*	I. albianthum S. Leiva	PER	known only from type collection
\mathbf{C}	I. cyaneum (Lindl.) M. L. Green	ECU, PER	
\mathbf{C}	I. cornifolium (Kunth) Miers	COL,4 ECU, PER	
\mathbf{C}	I. loxense (Kunth) Miers	ECU, PER (?)	
C*	I. schellerupii S. Leiva	PER	affined to $I.$ cornifolium by SDS
L	I. lehmannii Bitter	ECU, PER	
\mathbf{L}	I. squamosum S. Leiva & Quipuscoa	PER	affined to $I.$ $lehmannii$ by SDS
F	I. baumii S. D. Sm. & S. Leiva	ECU	
\mathbf{F}	I. calycinum Benth.	ECU, PER ⁴	
\mathbf{F}	I. fuchsioides Miers	COL, ECU	
\mathbf{F}	I. gesnerioides (Kunth) Miers	COL, ECU	
U	I. grandiflorum Benth.	ECU, PER	
\mathbf{U}^*	I. lilacinum S. Leiva & K. Lezama	PER	known only from type locality
U	I. nitidum S. Leiva & Quipuscoa	PER	
\mathbf{U}	I. tingoanum S. Leiva	PER	
U	I. umbellatum (Ruíz & Pav.) Hunz. ex D'Arcy	PER	
Hybrid	I. ayabacense S. Leiva	PER	known only from type locality; homoploid hybrid between <i>I. lehmannii</i> (<i>I. squamosum</i>) and <i>I. cyaneum</i> ²
Hybrid*	I. piuranum S. Leiva	PER	known only from type locality
Hybrid	I. stenanthum S. Leiva, Quipuscoa& N. W. Sawyer	PER	known only from type locality; possible hybrid between <i>I. cornifolium</i> and <i>A. arborescens</i> (L.) Schltdl. or other member of A clade ¹
Hybrid	Iochroma sp. indet.,?	PER	possible hybrid between A. arborescens or a member of U clade ¹
Excluded	I. parvifolium (Roem. & Schult.) D'Arcy	PER	more closely related to <i>Dunalia</i> Kunth. species than to <i>Iochroma</i> Benth ¹
Excluded	I. cardenasianum Hunz.	BOL	distantly related to other <i>Iochroma</i> species ¹ ; belongs to Datureae ³
Excluded	I. australe Griseb.	ARG, BOL	more closely related to <i>Eriolarynx</i> (Hunz.) Hunz. species than to <i>Iochroma</i> ¹

¹ Smith & Baum, 2006.

Table 1, several collections cannot be confidently assigned to a currently described species and may represent additional taxa deserving of species recognition (S. Leiva, pers. obs.).

Here we describe a new species of *Iochroma* from the cloud forests near Papallacta in northern

Ecuador. Phylogenetic analysis places this taxon in the northern Andean F clade, which contains two redflowered species (*I. gesnerioides* (Kunth) Miers and *I. fuchsioides* (Bonpl.) Miers) and another blue-flowered species, *I. calycinum* Benth. The new species shares with *I. calycinum* deeply pigmented flowers, which

² Smith et al., 2008.

³ Olmstead et al., 2008.

⁴ Shaw, 1998; specimens of these species from these countries have not been seen by the authors.

are variously described as purple, violet, and blue. Like other members of the F clade as well as the C clade, I. baumii S. D. Sm. & S. Leiva corollas have 10 teeth, sensu Shaw (1998), with five large teeth corresponding to the larger lobes and five smaller teeth alternate to the lobes. Also, similar to I. gesnerioides and I. calycinum, I. baumii produces masses of flowers in clusters along older branches, resulting in showy displays of hundreds of flowers in peak season. Its phylogenetic placement as one of the closest blue-flowered relatives to the two red-flowered Iochroma species will make continued study of I. baumii crucial to understanding the selective and genetic mechanisms underlying the evolutionary transition from blue to red pigmentation.

Iochroma baumii S. D. Sm. & S. Leiva, sp. nov. TYPE: Ecuador. Napo: near Papallacta, 00°22.076′S, 78°6.283′W, cloud forest, 2811 m, 4 Jan. 2005, S. D. Smith 476 with L. Lopez (holotype, MO accession #5448818; isotypes, F, MO accession #5875462, QCNE, WIS). Figure 1.

Haec species quoad corollam cyaneo-violaceam limbo 10-lobo lobis 5 majoribus cum 5 minoribus alternantibus *Iochromate calycino* Benth. affinis, sed ab eo inflorescentiis secus ramos vetustos aphyllos productis atque calyce tubuloso usque breviter urceolato viridi-cyaneo pubescente sub anthesi 4–9 mm longo et 3.8–6 mm crasso differt.

Treelet, (1.5–)2–4 m tall, with leaves clustered toward tip of branches and absent in mature growth; young stems, green, sometimes tinged with purple, pubescent with branched hairs, older stems glabrescent. Leaves $(6-)9-17 \times (2.5-)3-6$ cm, alternate, entire, elliptic to lanceolate, adaxial surface with branched hairs, abaxial surface densely covered in branched hairs; base cuneate; apex acuminate; petioles (0.8–)1.2–2.3 cm. Inflorescences axillary, typically on older, often leafless branches, rarely near the shoot apex, 6- to 12-flowered; pedicels 0.7-1.4 cm in flower, 1.5–2.5 cm in fruit, terete, pendulous, with few to many branched hairs. Calyx tubular to slightly urceolate, purplish green, with few to many branched hairs, $4-9 \times 3.8-6$ mm in flower, $9-12 \times$ 10–15 mm in fruit, with 5 broadly triangular lobes, sometimes with 2 fused to give the appearance of 4 lobes, shallowly divided in flower, becoming more deeply divided in fruit; corolla, tubular, flaring at the mouth, exterior deep blue-purple, with few to many simple or occasionally branched hairs, increasing toward the mouth, interior white with purple at the mouth, glabrous or with a few glandular hairs near the base, $28-45 \times 4-6$ mm at anthesis, 10-lobed, with 5 major lobes, acute in the apex and involute forming a

small hood, alternating with 5 minor lobes; stamens 5, included; filaments white or lilac, with simple and branched hairs, to 0.5 mm, on the basal 2/3, fused to the corolla on the bottom half (1–1.8 cm) with the free portion 1.3–2.4 cm; anthers 4–5.2 \times 1–1.5 mm, oblong, purple, longitudinally-dehiscent; ovary 3.3–4.8 \times 2–2.8 mm, pyriform, glabrous, with orange-yellow nectariferous disk, style 2.7–3.5 cm, stigma green, clavate, bilobed. Berry 1.2–1.7 \times 1–1.5 cm, green or green and purple at maturity with few to many sclerosomes, slightly conical, bottom 2/3 enveloped in accrescent fruiting calyx, style persistent (in fresh material); seeds 70 to 200 per fruit, 1–1.5 mm \times 1.4–1.7 mm, yellow, reniform.

Etymology. This species is dedicated to David A. Baum (1964–), professor of botany at the University of Wisconsin–Madison, in recognition of his contributions to understanding of the nature of species and his efforts to promote the incorporation of phylogenetics and tree-thinking in education at all levels.

Distribution and ecology. Iochroma baumii is endemic to the Andes of northern Ecuador and possibly Colombia. Its presence in Colombia is based on a single specimen collected in Caldas in 1946 (J. Cuatrecasas 23329, F); additional collecting effort will be necessary to determine if I. baumii persists there and in other parts of the country. *Iochroma* baumii shares its northern Andean distribution with other members of the F clade, but it is not known to occur in sympatry with any of these. In the type locality, I. baumii occurs in disturbed cloud forest habitats, such as pasture hedges, forest gaps, and roadsides. Population sizes appear small with individuals sparsely distributed, typically occurring no closer than 200 m apart. From the known collections, peak flowering occurs from December to May. Its flowers are unscented and appear protogynous like most Iochroma species (Smith et al., 2008). Despite its abundant displays, no pollinators have been observed during collecting trips. The related taxa (blue-flowered I. calycinum and red-flowered *I. fuchsioides* and *I. gesnerioides*) are principally pollinated by hummingbirds (Smith et al., 2008), but additional observations will be required to determine if *I. baumii* shares this pollination system.

IUCN Red List category. We currently categorized the conservation status of this taxon as DD (Data Deficient; IUCN, 2001). We have not to date conducted extensive surveys of the area where most of the collections have been made (the Napo Province of Peru), and thus the size of the populations is not well known. Also, the first authors have not collected

494 Novon

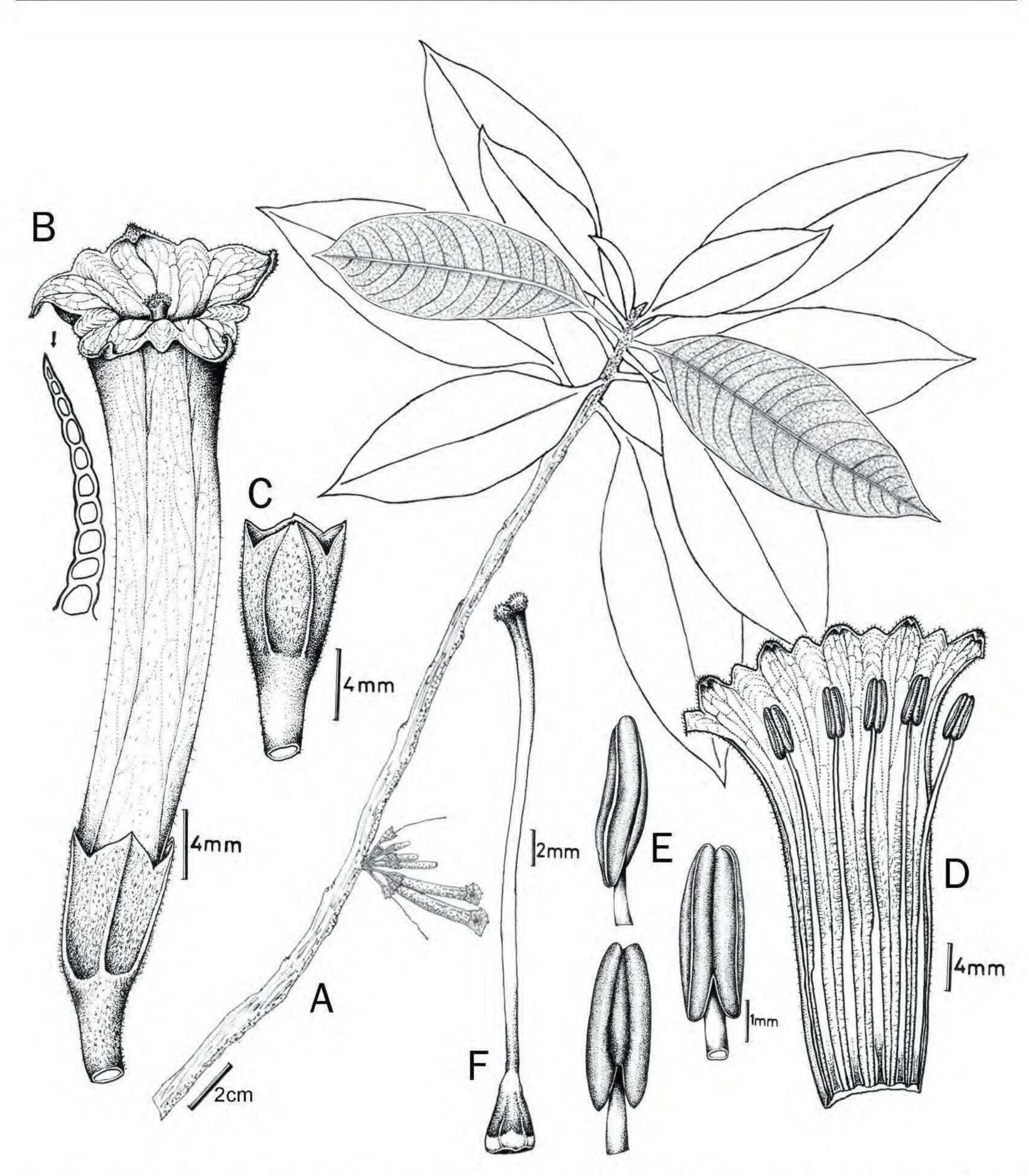


Figure 1. *Iochroma baumii* S. D. Sm. & S. Leiva. —A. Flowering branch. Leaf on the left shows the abaxial surface and on the right the adaxial surface. —B. Flower. Detail is shown for the simple hairs found on the corolla. —C. Calyx. —D. Inner corolla surface, showing the stamens. —E. Detail for the anthers, showing (clockwise from top) lateral view, adaxial view, and abaxial view. —F. Gynoecium. Drawn from S. D. Smith 477 with L. Lopez (MO) by S. D. Smith (A) and S. Leiva (B—F).

the species in Colombia, which may harbor additional populations.

Relationships. Within the well-supported F clade (Smith & Baum, 2006), the exact relationship of Iochroma baumii to I. calycinum, I. fuchsioides, and I. gesnerioides remains uncertain. The combined 3-gene analysis places it (identified as Iochroma sp. nov.) sister to the other blue species, I. calycinum,

with moderate levels of support; however, the three individual gene trees each show different relationships for these four taxa (Smith & Baum, 2006). Such a pattern may be expected if the lineages diverged in a short amount of time with differences in lineage sorting among genes. Phylogenetic analysis of additional individuals and genes will be required to identify the dominant phylogenetic pattern and the sources of discordance among gene trees.

Although the exact phylogenetic placement of Iochroma baumii is still unclear, the species is easily distinguished from other *Iochroma* species by several morphological features. First, two of the other blue species (I. calycinum and I. cornifolium (Kunth) Miers) have large inflated calyces in flower while I. baumii does not. It is also easily distinguished from the blue members of the U clade (e.g., I. nitidum S. Leiva & Quipuscoa and I. grandiflorum Benth.) that possess salverform corollas with five triangular corolla lobes compared to the tubular corollas with 10 teeth in *I. baumii*. The species is perhaps most readily confused with *I. cyaneum* (Lindl.) M. L. Green. The distribution of *I. cyaneum* is centered in southern Ecuador, but it is occasionally found in the north, possibly due to its cultivation as an ornamental. The two species can be distinguished by the fact that I. cyaneum retains leaves on older branches and most inflorescences are found near the shoot apex (as opposed to being on older branches in I. baumii). Also, *I. baumii* flowers have a distinctive hood on the major corolla lobes (Fig. 1), and its inflorescences have fewer flowers (six to 12 vs. 10 to 40 in I. cyaneum).

For specimens in which the flower color has faded or is not noted, there are several features that can be used to distinguish the deep blue flowers of *Iochroma baumii* from the red-flowered *I. gesnerioides* and *I. fuchsioides*. The calyx of *I. gesnerioides* is typically smaller, 3–5 mm, and *I. gesnerioides* often has larger numbers of flowers (10 to 25) per inflorescence, up to 120 according to Shaw (1998). *Iochroma fuchsioides* is largely glabrous, with at most a few simple hairs on flowers and vegetative tissue. For both red-flowered species, the flowers lack the hood on the major corolla lobes, and the anthers are often exserted in mature flowers while they are consistently included in *I. baumii*.

Paratypes. COLOMBIA. Caldas: Hoya del rio Otún, Peña Bonita, J. Cuatrecasas 23329 (F). ECUADOR. Napo: El Chaco Canton, Rio Oyacachi, Sector Nono, path betw. Oyacachi & El Chaco, 00°13′S, 78°02′W, J. L. Clark 3587 with J. Letham, D. Parion & M. Thurber (MO, QCNE); carr. Quito—Baeza—Cosanga—Napo, colecciones entre Baeza y Cosanga, A. Freire F. et al. 926 (F, QCA); Rd. Baeza—Papallacta, a few km. E of Papallacta, C. Padilla 1448 (MO, QCNE, WIS); Rd. Baeza—Papallacta, 00°22.780′S, 78°7.687′W, S. D. Smith with L. Lopez 477 (F, MO, QCNE, WIS).

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